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A gull's portrait

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Chapter 8

Synthesis

In this dissertation, herring gulls of a breeding colony on Texel were studied to better understand how behavioural differences among individuals affect fitness, with a special attention on how animals gather and allocate energy. We used 10 years of field data, supplemented with detailed GPS and behavioural data, to unravel the factors that play a role in behavioural decisions of free-living animals in a complex and changing foraging area. Studying different facets within one ecological system, helps to understand the importance of behavioural variation.

First, I will summarize the main results of each chapter and put my findings in a broader context. Then I will discuss the methodology used and consider possible alternatives. Finally, I arrive at the overall conclusions and will make some recommendations for further research.

Discussion of main results

The main findings of this dissertation are summarized below and in Fig. 8.1, in which the numbers correspond with those in the text below.

Part I

1. Dietary choice influences the reproductive success of herring gulls (Chapter 2). High caloric prey of anthropogenic origin are beneficial for reproductive success, while low caloric prey like blue mussels result in lower breeding success. However, despite the reproductive disadvantage most birds feed predominantly on low caloric mussels.
2. While high caloric prey of anthropogenic origin is beneficial for reproductive success, foraging effort required is higher than for other resources (Chapter 3). Gulls foraging for high caloric foods at sea (fishery discards) or in urban area (human food remains) spent more energy per hour because of more time in flapping flight per foraging trip than gulls foraging on low caloric prey (bivalves and terrestrial prey).
3. Individual herring gulls do not only differ in the diet they eat, but also in how faithful they are to their foraging patches (Chapter 4). Larger herring gulls had a higher level of site fidelity than smaller individuals. Nevertheless, there was no clear relation to energy expenditure; site faithful individuals neither spent more time in the breeding colony, nor had a lower energy expenditure compared to other strategies.
4. Habitat loss did not affect reproductive success on population level (Chapter 5). However, individuals within the population switched to an uncommon diet for this colony, probably due to higher competition on the remaining foraging habitat. These individuals had lower reproductive success than others.

Part II

5. Breeding is costly in terms of energy expenditure attributed to movement, but only during the period of chick rearing (Chapter 6 and 7). Herring gulls that skip a breeding opportunity can save 300 kJ per day compared to herring gulls that raise chicks. Saving energy one year can help to improve body condition for the next breeding opportunity.
6. Mass at age data were used to predict the total energy intake of growing chicks using the dynamic energy budget model (DEB). Predictions correlated strongly with measurements, which makes measuring food intake in the field not necessary. Total energy intake estimates of chicks can be used to calculate foraging effort of adult herring gulls with different foraging strategies.

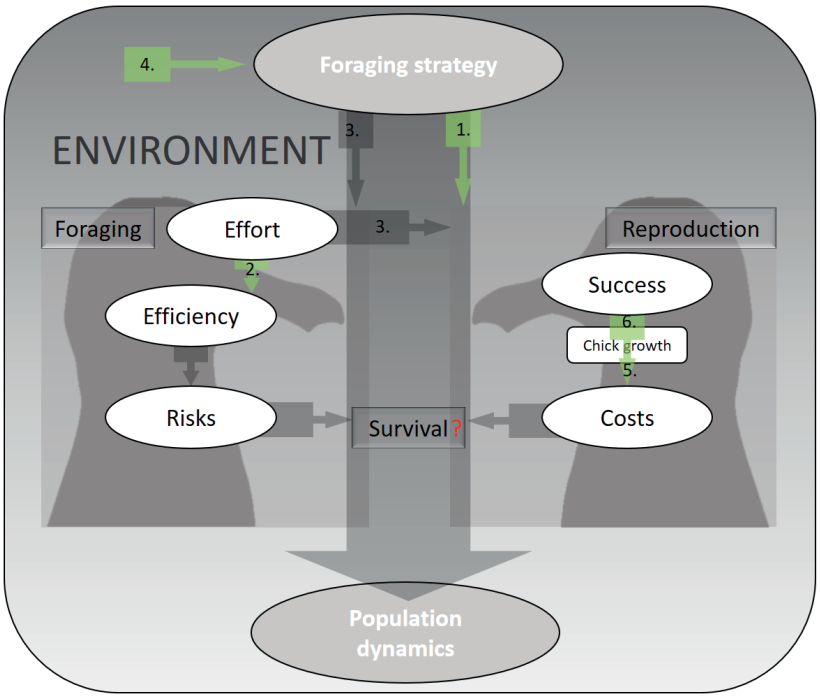


Fig. 8.1 Adjusted schematic overview of the framework of this thesis, which was presented in Chapter 1. A summary of the results are listed in the text on the previous page, the numbered results correspond with the numbers in this overview. Foraging strategy in this dissertation is studied as diet (1 & 4), habitat use (2) and as foraging site fidelity (3). When a relationship was found between two links in the scheme, the arrow is coloured green. When no relationship was found, only the number is indicated. Survival differences between individuals with different strategies is not known yet, and is a direction for future research.

Discussion of results

We showed that individual herring gulls differ in their diet, the habitat they visit and how faithful they are to foraging areas. Here, I discuss (1) how such variation in foraging strategies can be maintained in a population such as the herring gulls on Texel, (2) how variation in the population can be adaptive in a heterogeneous or changing environment, and (3) possible reasons why animals do not always adapt their behaviour according to changes in the environment.

1. Variation within a population

Herring gulls on Texel have a higher reproductive success when feeding their chicks with high caloric prey of anthropogenic origin, but foraging for these prey is energetically more expensive (Chapter 2 and 3). In contrast, herring gulls feeding their chicks with mainly low caloric bivalves, have a lower reproductive success but foraging on these prey is energetically cheaper. At the two extreme ends of the population, we have in theory individuals that breed successfully

and invest more energy in foraging and individuals that invest less in foraging and reproduce less successfully in a given year.

The differences between these two foraging strategies could be reflected in differences in life history traits (Stearns 1976). Life history traits reflect the trade-off between reproduction and survival in an environment with limited time and energy to support both (Williams 1966). This results in different life-history strategies between populations (Stearns 1992), but possibly also within populations (Réale et al. 2010). A 'slow-living' strategy is characterized by high survival and relatively low investment in reproduction while a 'fast-living' strategy is characterized by prioritizing reproduction over survival. A 'fast-living' life history is associated with more risk-taking behaviour which possibly results in their shorter lifespan (Réale et al. 2010).

The differences in life history strategies that are mainly studied on species level, can also explain variations in behaviour within the herring gull population on Texel. The successful breeders in our study system might suffer survival costs because of their high energy expenditure. Besides, they might suffer from risks associated with foraging for fishery discards or in urban areas, like possible injuries or entanglement in fishing gear (Favero et al. 2010) or a potentially higher risk of infection by diseases in urban areas (Bradley and Altizer 2007). While the less successful breeders do not suffer from these survival costs of energy expenditure and risks while foraging on predictable bivalves, possibly resulting in a longer lifespan. In the long-run, both strategies may result in similar lifetime reproduction and might thus be equally good strategies in terms of fitness.

Foraging strategies can also have similar fitness, when there are no clear short-term benefits or differences in life history traits. The results of chapter 4 of this dissertation show that individuals that differ in the level of site fidelity do not differ in the time they spent foraging or the time invested in reproduction, but larger gulls are more likely to be site faithful. Foraging strategies can be determined by morphology. Size affects energy expenditure in gulls and other species (Speakman 2005) and larger individuals are more likely to be dominant (Monaghan 1980). Therefore, they can more easily secure a foraging site in a competitive situation. Besides, flying is more expensive for them in terms of energy expenditure. It might be more rewarding for these larger individuals to be site faithful to avoid costly flight costs. For smaller individuals, moving between foraging patches is less expensive and therefore possibly less rewarding to invest energy in requiring a position in the dominance hierarchy.

Behavioural variation between individuals without clear fitness consequences can also be maintained by a mechanism called 'negative frequency dependent selection'. This mechanism suggests that as long as a population consists of different phenotypes in a certain frequency, individuals have the same fitness. As soon as one strategy increases in frequency in the population, individuals with that strategy experience disadvantages in for instance food intake

and ultimately fitness, creating advantages for individuals with other strategies (Fitzpatrick et al. 2007). However, I do not think that this mechanism influences variation between individuals in gulls. The examples of populations in which this mechanism plays a role often consist of individuals with extreme differences in their strategy resulting in a bimodal distribution. In our study on foraging site fidelity, the gulls show a unimodal distribution in their strategies, instead of a bimodal one. Two studies that investigated this mechanism in birds, could also not find evidence for this theory (van de Pol et al. 2010, Kurvers et al. 2012).

2. Variation in a fluctuating or heterogeneous environments

The advantages and disadvantages of strategies are not static and can fluctuate over time, as the environment fluctuates by natural causes or human disturbances. As such, a strategy that is very advantageous in one environment can have disadvantages when its environment has changed, resulting in fluctuating selective pressures. For instance, a long-term study of 26 years on a population of oystercatchers *Haematopus ostralegus ostralegus* showed that selection fluctuated between years. Generalists were slightly in favour in most years in terms of survival, but were strongly selected against in rare harsh winters (van de Pol et al. 2010). Another study on this species, but in a different region did not find differences in survival between individuals that varied in strategies (Durell 2007). In black-browed albatrosses *Thalassarche melanophrys*, females that foraged closer to the colony had higher fitness than females foraging further away, but only in years with high estimated food availability. In years with low estimated food availability, females foraging further away were in favour in terms of fitness (Patrick and Weimerskirch 2014b).

In a similar way, particular prey types can be relatively stable or unpredictable in amount or quality and thus require a different foraging approach. In the studied population, bivalves provide a predictable and stable food source, and are available during low tide. Other prey items have a less predictable rhythm; fishery discards are primarily available on weekdays and the availability of earthworms is dependent on rain. Individuals that forage on less predictable prey, should logically have other foraging options available, while this is not necessary for individuals that forage on more predictable prey. The first should therefore have a wider knowledge of the environment, while the second has possibly a competitive advantage in knowing one specific environment very well.

3. Pre-programmed individuals in a changing world

Above, I described several mechanisms in which variation can be maintained in a population, and how this can actually be advantageous to deal with a heterogeneous or changing environment. Several studies have suggested that generalist predators are increasing in urban areas because they have a broad diet spectrum and are thought to be more flexible and thus better in exploiting new food resources than specialist species (Chautan et al. 2000, François

2002, Gompper 2002, Contesse et al. 2004, Mitchell et al. 2004, Rock 2005, Soldatini et al. 2008). The foraging environment of herring gulls is also changing. Two decades ago, open dump sites and fishery discards provided still plentiful foods for gulls. However, open landfills have decreased particularly since the 1990s; the open dumpsite on Texel was closed in 1991 and so were many others in the Netherlands and Europe (Kohler and Perry 2005, Camphuysen 2013, European Environment Agency (EEA) 2016, Rijkswaterstaat 2016). Similarly, the availability of fishery discards declined due to a lower fishing effort since the late 1990's and stricter legislation towards discarding bycatch (Poos 2010, "Factsheet : North Sea brown shrimp" 2011, Camphuysen 2013, Borges 2015). Are the generalist herring gulls able to quickly adapt as suggested for other generalist predators (Devictor et al. 2008, Clavel et al. 2011)?

The gulls have indeed changed their foraging behaviour, their diet contains now proportionally more mussels and less anthropogenic prey than at the start of the monitoring on Texel (Chapter 5, Fig. 5.2). However, they did not change in such a way to prevent a decrease in fitness over time, as mussels are insufficiently nutritious for chick growth (Chapter 2). Second, we show that raising chicks is costly in terms of energy expenditure (Chapter 6), but individuals do not increase their foraging effort when energetic needs of their chicks grow despite low reproductive success of the breeding colony. Third, we show that individual herring gulls do change their (short-term) foraging behaviour when part of the foraging habitat is lost, but some individuals switched to a clearly unsuccessful strategy (Chapter 5).

One way to adapt to the worsened conditions in resource availability around the breeding colony on Texel would be to move to another breeding location closer to high caloric food and reduce foraging costs. However, the number of breeding birds stayed stable over the time that this breeding colony was monitored and colour ringed adult birds are very faithful to their breeding colony, often even coming back to the exact location of their former territory (Camphuysen 2013). Why do herring gulls, as a species, seem to adapt well to increasing urbanization and landscape fragmentation, but on an individual level appear to have difficulties changing foraging habits and do not move to a better breeding location that is situated closer to the food they need for reproduction? Here, I hypothesize that plasticity of gull behaviour is limited during the lifetime of an individual.

Seabirds have a long period of immaturity (Dobson and Jouventin 2007), in which they are generally more explorative than adults (Riotte-Lambert and Weimerskirch 2013, Orben et al. 2018). This explorative behaviour might help them to gain experience that they can use later in life; for example, seabirds gain knowledge during immaturity which makes them more efficient foragers as adults (Maclean 1986, Riotte-Lambert and Weimerskirch 2013). Over time, birds often become less variable and more repeatable in their (foraging) behaviour with increasing age and experience (Wakefield et al. 2015, Votier et al. 2017, Campioni et al. 2019, Kok et al.

2019) thereby developing distinct migration and foraging strategies (Phillips et al. 2017, Campioni et al. 2019). This so-called behavioural canalization suggests that animals develop behavioural traits based on the conditions experienced at the start of development, but become less flexible at a later age. Environmental information gathered during the early life can thus have lifetime consequences on foraging behaviour (Dall et al. 2012). The increase in repeatability and decrease in flexibility might be adaptive, when birds forage in areas that yield predictable prey availability over longer timescales (Bradshaw et al. 2004, Wakefield et al. 2015). For instance, reproductive success in black-browed albatrosses *Thalassarche melanophris* was higher in females that were site faithful to their foraging habitat in a given year, and between years individuals with higher site fidelity tended to have higher reproductive success (Patrick and Weimerskirch 2017). Behavioural canalization can be adaptive in an environment that is relatively predictable, but when the environment changes rapidly there may be dire consequences for individuals that do not retain enough behavioural plasticity to adapt to environmental change within their lifetime.

Implications for methods

Studying animals in their natural environment allows one to observe how animals adapt their behaviour to a variety of biotic and abiotic factors, which makes studying free-living animals challenging. However, studying animals in their natural environment is important, because an animal has to adapt its behaviour based on all these biotic and abiotic factors and not on stable laboratory conditions. We applied standard field methods, already in use for decades, but also used recently developed approaches. Here, we discuss shortly some of these methods and compare them to possible alternatives.

In chapter 2, we used the analysis of regurgitates to investigate the diet of herring gulls in relation to reproductive success. This method is non-invasive for the gulls as animals do not have to be caught and it is possible to gather many regurgitates per nest site. Also, it gives a good indication of the diversity of prey in the diet. However, it is possible to miss prey types that do not have hard non-digestible parts that are regurgitated by the gulls. The pacific oyster *Magallana gigas* is such a prey that will be missed by the regurgitate method, as gulls drop these large shells on hard substrate and only eat the soft flesh. The pacific oyster is an invasive species that has spread rapidly in the Wadden Sea. Learning about the frequency of this specific prey type in the diet of predators is of interest, as that can tell us something about the importance of this new species in the ecosystem.

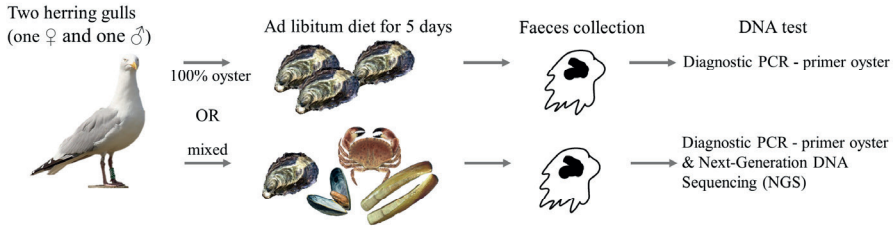
We tested the use of DNA markers on faeces to detect soft prey types like the pacific oyster in a small laboratory study with two herring gulls (Box 8.1). Both birds received two types of treatment for several days in a row; they were either fed with 100% oyster meat, or received a mixed diet which contained 25% oyster for several days to imitate a more natural setting, as

gulls often eat more than one type of prey. Faeces of these two gulls were collected daily and stored. Subsequently, a diagnostic PCR (Philippart et al. 2014) with a tested oyster-primer was done. With this method, it was possible to detect oyster DNA in the faeces. However, not all faeces of the 100% diet gave a positive result. Besides, we found a big difference between the two tested individuals. This finding suggests that individuals vary in their gut flora which can influence the results. Therefore, using diagnostic PCR to identify prey in faeces needs to be tested more thoroughly in the laboratory before it can be used in the field. Another way of measuring the diet by using DNA in the faeces is by performing next generation DNA sequencing in combination with metabarcoding (Pompanon et al. 2012)(Box 8.1). With this method, one can test for multiple prey, but only the species of which the genetic barcode is known.

Gathering regurgitates at a nest site has another disadvantage; one is only able to learn about the diet of a herring gull pair and not about the diet of an individual. A way of gathering information about the individual, is by monitoring habitat use. We used two methods to monitor habitat use; colour rings and GPS trackers. Colour rings can be used to measure both survival and habitat use and are instrumented in large numbers because of their low price and little impact on the animals. However, the re-sighting rate is dependent on the effort of observers; some areas are more accessible than other areas. Also, it is very hard to re-construct how animals spend their time by only observations. Monitoring time-energy budgets is possible with bio-logging. In this dissertation, several studies were based on the data of GPS trackers. GPS trackers with accelerometers provide information on the habitat use of the gulls (independent of observer effort) and on time and energy budgets. These trackers have provided new information and insights on the behaviour of animals that could not be measured before. However, there is still a lot to discover. Data gathered during the study period of this thesis consists of a wealth of information on detailed behaviour of gulls. Individuals with different strategies do for instance differ in daily foraging patterns (Box 8.2). This can have implications on the co-operation with the breeding partner during parental care. For instance, breeding pairs that both forage on intertidal prey are constrained by the tide and thus have to cooperate in such a way that they can both go out for foraging during low tide without leaving brooded eggs unattended. Breeding pairs that do have the same daily rhythm might be able to share foraging and breeding time in a better way. Good cooperation between breeding pairs is important and seems to be related to reproductive success in a recent study on lesser black-backer gulls *Larus fuscus*. Breeding pairs that had a more equal division of parental care during incubation, had a greater reproductive success when their brood was experimentally enlarged compared to pairs that divided the work less equally (Kavelaars et al. 2019).

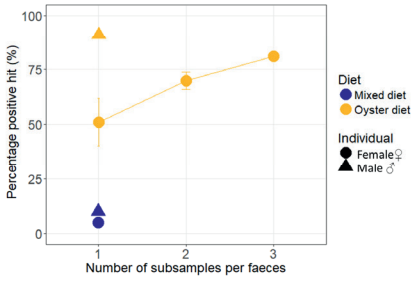
Box 8.1 Overview of an exploratory study on diagnostic DNA tests on gull faeces. This study was conducted in collaboration with Rohy Berghuis, Kees Camphuysen, Boukje Heidstra and Judith van Bleijswijk.

AIM: to evaluate a diagnostic DNA test on gull faeces to detect oyster consumption



RESULT diagnostic PCR - primer oyster

- 80-90% positive hit on oyster diet by using 3 subsamples
- About 10% positive hit on mixed diet
- Individual differences in success rate (confirmed with diagnostic PCR on 100% mussel faeces)



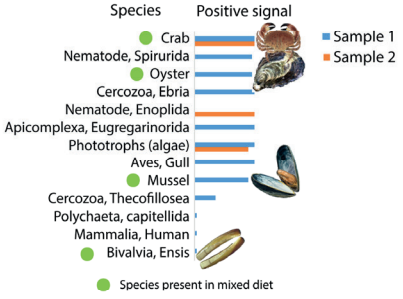
Faeces (% positive hit for oyster) after analyses of 1, 2 or 3 subsamples. Gulls were fed on oyster diet (#faeces 23 for ♀ and 27 for ♂) and mixed diet (#faeces 49 for ♀ and 37 for ♂).

- DNA markers can be used to detect oyster, but more subsamples are needed for optimal detection
- Individual differences are found in the success rate of the PCR, differences in gut flora might influence the result

RESULT Next-Generation DNA Sequencing of mixed diet

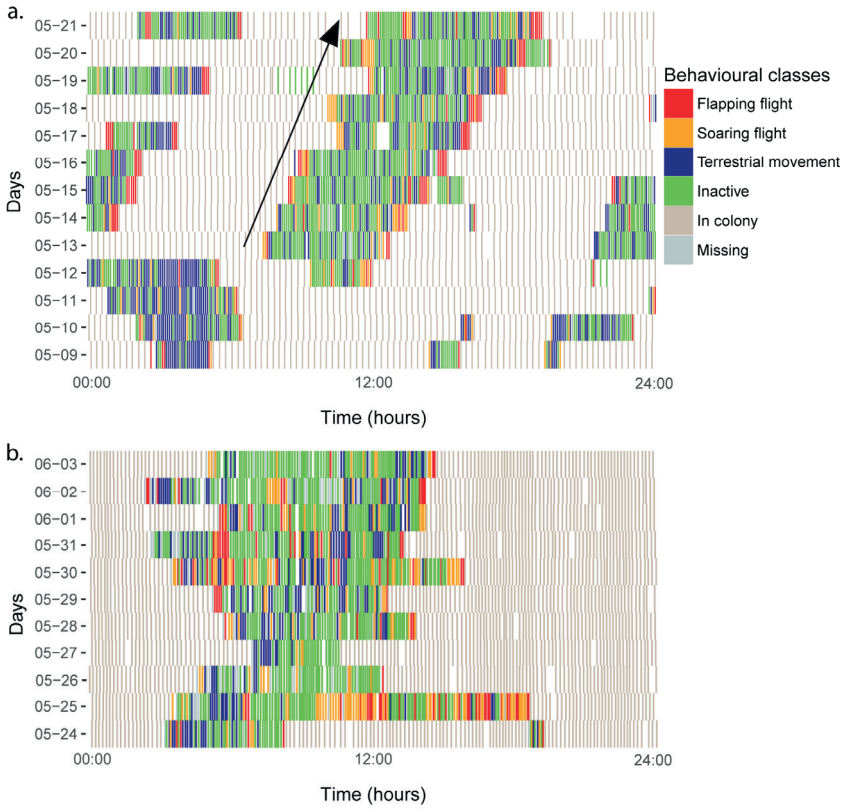
NGS on 2 faeces samples of ♀

- All prey types of mixed diet are detected in sample 1
- Results NGS correspond with diagnostic PCR (positive for sample 1 and negative for sample 2)



- NGS results correspond with the diagnostic PCR results of the same faeces samples
- NGS does not show all prey types of the mixed diet in both faeces samples. Even in a mixed diet, gulls might have faeces with remains and DNA of only one prey type

Box 8.2 Daily rhythms of two individual herring gulls carrying GPS trackers during the incubation period. On the Y-axis from low to high preceding calendar days. On the x-axis time of the day from 00:00 until 24:00. Colours indicate the behaviour of the two individuals, or the time they spent in the colony when no behaviour was registered. a. An individual that forages mainly at breakwaters on blue mussels. The arrow indicated that the bird left the colony on average an hour later every day, following the changing tide over the days. b. An individual that has a more mixed foraging strategy using both urban areas as breakwaters. This bird has a more repetitive daily rhythm; leaving the colony in the middle of the night and coming back in the early afternoon.



Conclusions and outlook

The work presented in this dissertation shows the consequences of different foraging and breeding decisions for proxies for fitness. In this final chapter, several possible mechanisms which could promote variation in these decisions were discussed. Furthermore, recent environmental change can result in natural selection of generalist species or individuals. However, to be able to make conclusions about mechanisms and to predict possible selection due to environmental change, more studies are needed.

In this thesis, we were interested in foraging strategies in relation to fitness proxies, which was the reason to study individuals while breeding. However, the breeding season is only a short part of an animals life. The conditions that an animal experiences outside the breeding season, can also highly influence the body condition of an animal (Harrison et al. 2011). The tracking data gathered during this dissertation, opens up possibilities to study this so-called carry-over effects. For instance, are individuals that are site faithful during the breeding season also site faithful at other foraging sites and provides this behaviour them with a long-term energetic advantage (in contrast to our findings during the breeding season, Chapter 4).

Another line of research should focus on survival of individuals with different foraging strategies (Fig. 8.1). In this way, we could answer the question whether animals foraging on high caloric prey with high breeding success have indeed a lower life expectancy than animals that forage on low caloric prey. And whether this results in similar lifetime reproductive success. Or we may find out that individuals that vary in foraging strategies do not differ in survival. Some herring gulls might just have a competitive advantage, and are able to claim better quality food for their young. This could be important when certain habitat is affected by human activities. Recently, several wind parks are being built in the North Sea and there are concerns whether seabirds foraging at sea are affected (Dierschke et al. 2016). When fishery discards-specialists have a higher lifetime reproductive success, because they are able to claim the beneficial prey types for chick growth, loss of such an individual has a larger effect on population level than the loss of a mussel specialist with potentially lower lifetime reproductive success. Survival analyses are already within reach with the large amount of re-sighting data of individuals with colour rings that have been gathered over the last 14 years.

Such analyses have been done on oystercatchers in which two papers examined whether survival differed between individuals (Durell 2007, van de Pol et al. 2010). For instance, van de Pol and colleagues (2010) found that survival can differ between individuals depending on their foraging strategy, but which strategy is selected against depends on the weather conditions. Also survival between spoonbills *Platalea leucorodia leucorodia* that vary in migration strategies has been examined with the use of re-sighting data (Lok et al. 2015). Understanding

both the survival and the breeding consequences of foraging strategies, could give us a better understanding of what the implications of these different strategies are on a population level.

General reflection

Humans have a curious nature and they love to find reasoning in animal behaviour on the basis of environmental and genetic criteria. But maybe we have to admit that an individual animal has just as much complexity as any individual human. Environmental conditions can affect us, sometimes in similar directions, but even identical twins growing up in the same family develop as individuals with different personalities (Torgersen and Janson 2002). Every individual, both human and non-human, will experience the environment in a different way. It will unfortunately be very difficult - if not impossible - to find rules and algorithms that explain all variation in animal behaviour. However, we might be able to shed some light on the patterns and mechanisms, which will enable us to admire and enjoy the diversity and complexity in populations and societies even more.